Computational Models of Adult Neurogenesis

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Abstract

Experimental results in recent years have shown that adult neurogenesis is a significant phenomenon in the mammalian brain. Little is known, however, about the functional role played by the generation and destruction of neurons in the context of and adult brain. Here we propose two models where new projection neurons are incorporated. We show that in both models, using incorporation and removal of neurons as a computational tool, it is possible to achieve a higher computational efficiency that in purely static, synapse-learning driven networks. We also discuss the implication for understanding the role of adult neurogenesis in specific brain areas.

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I. ADULT NEUROGENESIS AND COMPUTATION

Adult neurogenesis (AN), that is, the incorporation of new neurons in adult brains, has been documented in the mammalian olfactory bulb and the dentate gyrus, as well as in in a variety of subcortical areas and different areas of the neocortex, but with less significance [1, 2, 3]. A number of observations point to a functional role for AN, in particular the increase in proliferation after exposure to novel environments [4, 5], and the incorporation of new neurons as functionally connected elements [6]. We have recently introduced the first computational model of adult neurogenesis in the olfactory bulb [7], showing that the death and incorporation of inhibitory (granule) interneurons is enough to achieve the orthogonalization of an input ensemble, a task the olfactory bulb is assumed to be involved in [8]. The model predicted an initial wave of massive cell death for newly incorporated neurons, followed by a constant, small and protracted background of death. Interestingly, these qualitative predictions were subsequently confirmed by experiments [9]. This model, however, was not able to account for the possible computational necessity of AN, given that similar results can be obtained by synaptic learning. We are nevertheless interested in proving the hypothesis that AN is a required solution to specific problems found by evolution, as opposed to an evolutionary vagary. We present in this letter two models that provide evidence for this hypothesis. We will discuss first a model in which the replacement of neurons is based on their level of activity, displaying interesting information-theoretic properties. We will later introduce a model in which the replacement is based on a measure of correlation between neighboring neurons; this second model shows interesting properties related to the convergence to minimal distortion of neural maps.

II. REPLACEMENT MODELS

The activity-based replacement model consists of a network of projection units that learn to represent an input ensemble based on a winner-take-all approach (WTA). This model is related to the Growing Cell Structure (GCS) algorithm introduced by Fritzke [10], but unlike it has a simple physiological interpretation. The GCS approach requires the incorporation of new neurons with specific synaptic weights, derived from those of already incorporated neurons; in our algorithm, this "teleological" requirement is not present.

The training proceeds as follows: upon presentation of an input $\mathbf{X}_n$, a winner unit is selected such that, $\mathbf{W}_k = \min_i |\mathbf{W}_i - \mathbf{X}_n|$. The winner and the runner-ups are updated following a standard Hebbian rule: $\Delta\mathbf{W}_k \propto \mathbf{X}_n - \mathbf{W}_k$, and $\Delta\mathbf{W}_i \propto (\mathbf{W}_i - \mathbf{W}_k)f(|\mathbf{W}_k - \mathbf{W}_i|)$, where $f()$ is a non-linear decreasing function of its argument; here we will choose and exponential. We introduce here the novel component of the algorithm. First, a winning rate is computed for each unit, $w_i^n = 1$ if $i = k$, 0 otherwise, $\Rightarrow \omega_i = \langle w_i \rangle_n$, intended to capture the unit's recent activity. Based on this value, the units are replaced. This is done probabilistically, $p(\text{death})_i \propto 1 - \omega_i$. At the same time, new neurons arrive constantly, with a probability $p(N + 1) = \lambda$. The newly arrived units are not immediately connected: they are allowed to participate of the competition process, but do not become part of the representation ensemble until a trial period τ has passed. In this way, the number of output units is always bounded, and new neurons are allowed to find a good configuration.

The results of the simulation are shown in Fig 1-A,B. Different input ensembles consisting of 100 elements are drawn from a uniform distribution on the unit $100D$ hyper-sphere. The network is initialized with an arbitrary number of output units ($50[\circ]$ and $150[\circ]$ in this case), and is trained with a random sequence of input exemplars. As small amount of noise is added to the input exemplars, but this is not a determining factor. Panel A shows the evolution of the mutual information between the input and the output ensembles, relative to the maximal mutual entropy (the entropy of the input in this case). The mutual information here is measured as in a discrete channel, using only the output units, as $H(\mathbf{X}, \mathbf{W}) = H(\mathbf{W}) - H(\mathbf{W}|\mathbf{X})$. We observe that indeed the network evolves towards maximal mutual information, for both low and high initial number of units. This is expected of a network implementing the Hebbian component of the algorithm. Panel B is however more surprising: it shows that the network evolves towards a number of units equal to the number of input clusters, independently of the initial number of units. This is indeed a robust feature, independent also of the total number of input clusters.

Given that mutual information maximization can be equally achieved by a non-modifying Hebbian network, what is the advantage of implementing a network like this one? A key point here is the ability of the network to track the number of input clusters in the number of output units. A simple analysis of a the discrete channel defined by the network shows that, for a given number of inputs M and network size N, the maximal mutual information normalized by the input entropy scales like $\log N$ for $N < M$, and is 1 when $N \geq M$. At the
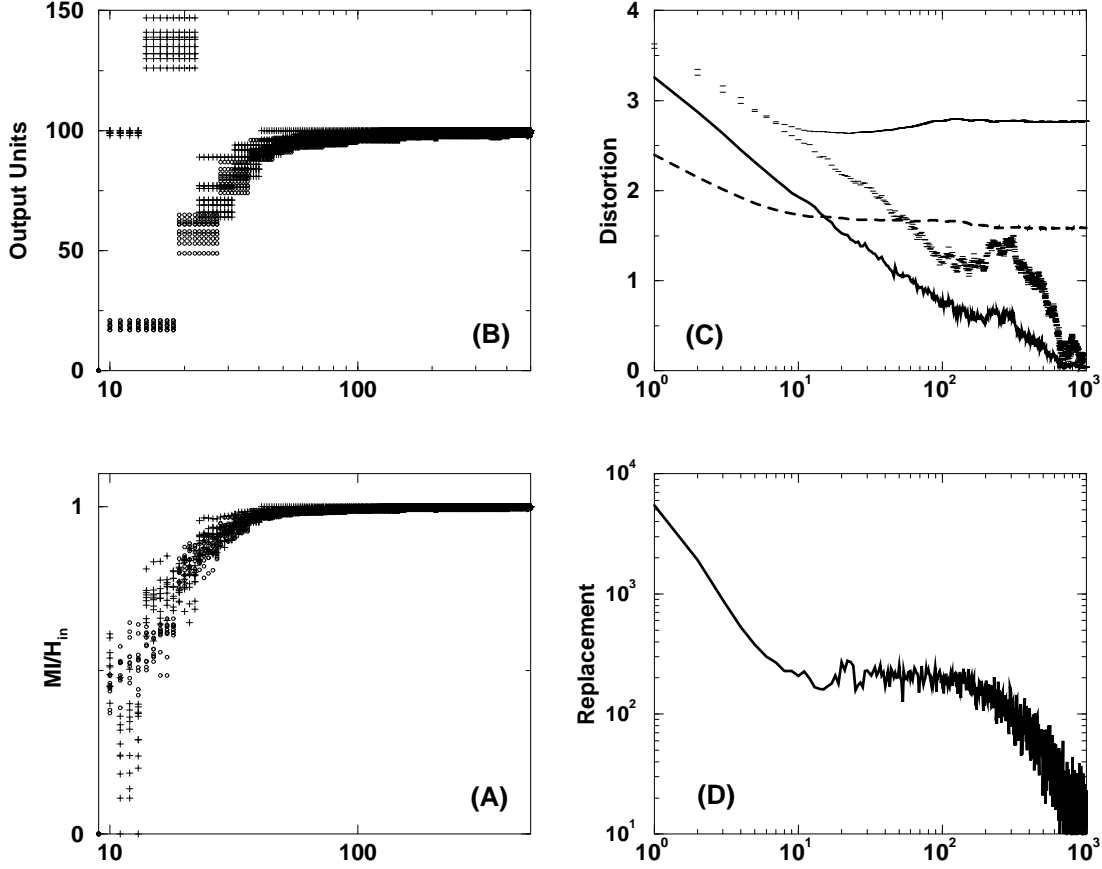
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FIG. 1: A: Mutual Information of activity-based model. B: Total number of output units in the same model; x-axes are iterations x10^3. C: Distortion averaged over initial configurations for correlation-based model (solid line), and simple elastic model (dotted line). Dashes are one standard deviation, and the x-axis is iterations. D: Average replacement rate for the correlation-based model

same time, the redundancy of the output, defined as $H(\mathbf{W}|\mathbf{X})$ is 0 when $N < M$, to then scale as $\log N - \log M$. This shows that a WTA-like network with the same number of units as number of inputs in the input ensemble (the *cardinality*) can at the same time maximize the mutual information and minimize the output redundancy. Both features are relevant in the context of brain processing [11]; in particular, minimizing the total number of outputs without compromising the mutual information can reduce the wiring and crosstalk in the target network, if at the expense of maintaining a costly mechanism like AN, and in the context of an unknown and possibly changing cardinality of the input ensemble.

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The model presented above shows one possible advantage of combining classical synaptic learning with AN. One limitation of this model is the the task required from the network is fairly simple, and lacking therefore generality. In what follows we will present a different model, in which the replacement of units is driven by correlated activity, and implementing a less simple form of computation, i.e. topology-preserving mapping. This correlation-based replacement model is based on the elastic net introduced in [12]. The goal of the network is to represent the input space in a topographically order fashion, such that nearby units in neural space have similar receptive characteristics. The network differs from the previous one in that no winner needs to be computed, and neighboring units influence each other. Formally, the update rule is: $\Delta \mathbf{W}_i = \alpha A_i(\mathbf{X} - \mathbf{W}_i) + \beta \kappa (\mathbf{W}_j - \mathbf{W}_i)h(d_{ij})$, where $A_i = e^{-(\mathbf{X}-\mathbf{W}_i)^2/2\kappa^2}/\mathcal{N}$, and $\mathcal{N} = \sum_j e^{-(\mathbf{X}-\mathbf{W}_j)^2/2\kappa^2}$, can be interpreted as a normalized activity, d_{ij} is the distance between units i and j in neural space, and $h()$ a monotonically decreasing function of its argument. In many cases, as in here, a simpler version is used where only the immediate first neighbors of each unit are considered. In this case, the second term of the update equation reads $\beta(\mathbf{W}_{i+1} + \mathbf{W}_{i-1} - 2\mathbf{W}_i)$. It is interesting to notice that the update equation minimizes an energy function than can be computed by simple integration, $E = -\alpha\kappa \sum_n \log \sum_i e^{-(\mathbf{X}_n - \mathbf{W}_i)^2/2\kappa^2} - \beta \sum_i (\mathbf{W}_{i+1} - \mathbf{W}_i)^2$. The elastic net has been used in a variety of optimization problems, like the travelling salesman problem, and also in simulations of cortical maps. It is well known, however, that as many optimization algorithms, the elastic net can get trapped in local minima depending on the complexity of the input space. To illustrate this phenomenon, we implemented and elastic net of 100 units tasked with learning an input space consisting of 100 exemplars distributed on a two dimensional space as $y_i = 50 \sin(x_i \pi/35 + \pi/2) + 50$. Without scheduling of κ [12], the elastic net can find an optimal solution only in less the 1% of initial conditions (Fig. 2). In contrast, the same network, with the addition of the correlation-based replacement, is able to find the optimal solution under any initial condition. The algorithm is as follows: each unit computes a correlation-based or "stress" variable, whose evolution is defined as $\dot{s}_i(t) = \gamma[\sum_j (\mathbf{W}_i - \mathbf{W}_j)^2 h(d_{ij})]^{1/2} - \mu s_i(t)$, where γ and μ are arbitrary parameters, and the initial condition for new neurons is $s_i(t)|_{new} = 0$. When the "stress" reaches a threshold, the unit is "replaced" by a new one with an arbitrary distribution of synaptic weights, $s_i \geq S_T \Rightarrow reset[\mathbf{W}_i]$. The results of the simulation are presented in Panel C, where the ensemble average over initial conditions shows a linearly decreasing behavior in semilog scale.

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Although the individual evolution for different initial configurations can vary dramatically, for our toy example they all converge to minimal distortion in finite time, in sharp contrast with the pure elastic net algorithm. Panel D shows the evolution of the replacement rate, defined as the number of replaced units per cycle. It displays a fast (power-law) initial decay, followed by a long exponential tail; interestingly, the same qualitative features are observed both experimentally and computationally in the olfactory bulb, as mentioned above.

In summary, we have shown two novel mechanisms that suggest that AN may be a necessary computational tool used by brain structures whenever (a) an input ensemble of discrete elements and non-stationary cardinality needs to be processed (the activity-based model), or (b) a topographic map of a complex input space needs to be formed with minimal distortion (the correlation-based model). The first feature maybe relevant for the neural processing required by the High Vocal Center, a brain area of songbrids were replacement correlates with song modification [3]. The second feature maybe important for the generation of an adaptive neural map in the Dentate Gyrus (DG) of the Hippocampus. We can only speculate at this point, but the local circuitry of the DG is complex enough to support a physiological implementation of the correlation-based algorithm [13], and the correlation of replacement with exposure to novel environments [4] is compatible with our model.

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